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NEW CRANIAL MATERIAL OF THE RARE DIADECTID *DESMATODON HESPERIS* (DIADECTOMORPHA) FROM THE LATE PENNSYLVANIAN OF CENTRAL COLORADO

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Abstract

Additional skull and lower jaw material of the rare diadectid *Desmatodon hesperis* is described from the Late Pennsylvanian Badger Creek locality in the Sangre de Cristo Formation of central Colorado. A new partial maxilla suggests that the more primitive degree of molarization of the cheek teeth—one of the features used to distinguish *D. hesperis* from *D. hollandi*—may actually reflect a difference in maturity rather than a taxonomic character. Other characters used to distinguish these species remain unchallenged. The new material further demonstrates that the cranial morphologies of *D. hesperis* and *Diadectes* are nearly alike, with only the marginal and palatal dentitions providing a substantial means for distinguishing between them. Previously described differences between the maxillary dentitions in juvenile and adult stages of growth are further documented. Among the *D. hesperis* elements described for the first time here are adult specimens of the dentary and nearly complete lower jaw; the cheek teeth exhibit the same primitive degree of molarization as the maxillary cheek teeth when compared with those of comparably sized adult specimens of *Diadectes.* The presence of teeth on the transverse flange and twice as many teeth of smaller and variable sizes in the medial tooth row of the palatal ramus of the pterygoid also separates *D. hesperis* from *Diadectes.* The lower jaw of *D. hesperis* can also be contrasted with those of comparably sized *Diadectes* specimens by its much shallower depth, reflected also in the shape of the adductor fossa and medial fenestra, and its much lower labial parapet of the dentary. A previously reported occurrence of *Desmatodon* aff. *D. hollandi* from the Late Pennsylvanian Cutler Formation of El Cobre Canyon, New Mexico, may represent only the second occurrence for the species and the third for the genus.

Introduction

The late Paleozoic tetrapod suborder Diadectomorpha, including the families Diadectidae, Tseajaiidae, and Limnoscelidae, is now widely accepted as the sister group of all amniotes (Gauthier et al., 1988; Panchen and Smithson, 1988; Berman et al., 1992; Laurin and Reisz, 1995). In this context, the study of the diadectomorphs takes on great significance as a key to better understanding the origin and early radiation of late Paleozoic amniotes. Most recently, Berman et al. (1992) presented a novel hypothesis that the Diadectomorpha and synapsids form a sister clade to that including all other amniotes. If correct, this relationship would confer amniote status to the Diadectomorpha, a longstanding, controversial topic (Romer, 1946, 1964; Fracasso, 1987; Gauthier et al., 1988; Panchen and Smithson, 1988; Laurin and Reisz, 1995). The conclusions of Berman et al. (1992) were based on a restudy of the cranial anatomy of *Diadectes, Tseajaia,* and *Limnoscelis,* the type genera and only representatives known by adequate skull material of the three recognized diadectomorph families. In the same study an analysis of diadecto-

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morph phylogeny was also attempted. The results recognized only one cranial character each to support the hypotheses that the Diadectomorpha, as defined above, is a natural group, and that *Diadectes* and *Tseajaia* share a more recent common ancestor than either does with *Limnoscelis.* A second recent study (Sumida et al., 1992) of the atlas–axis complex of primitive tetrapods identified a further synapomorphy of the Diadectomorpha.

Any phylogenetic analysis of the Diadectomorpha suffers from reliance on so few taxa. The family Tseajaiidae is monotypic and based on a single species, *Tseajaia campi,* represented by complete skeletons from the Early Permian (Vaughn, 1964; Moss, 1972) and Permo–Pennsylvanian (Berman, 1993). The Late Pennsylvanian *Limnoscelis paludis* and *L. dynatis,* which are represented by a complete skeleton and the greater part of a skeleton, respectively (Williston, 1911*a,* 1911*b*; Romer, 1946; Fracasso, 1987; Berman and Sumida, 1990), provide essentially the entire basis of the definition of the Limnoscelidae. Four other Pennsylvanian or Early Permian limnoscelid taxa have been described on the basis of very fragmentary specimens (*Limnosceloides dunkardensis* Romer, 1952; *Limnoscelops longifemur* Lewis and Vaughn, 1965; *Limnosceloides brachycoles* Langston, 1966; and *Limnostegis relictus* Carroll, 1967). *Romeriscus periallus,* described by Baird and Carroll (1967) as a limnoscelid, has been restudied recently by Laurin and Reisz (1992), who concluded that the genus cannot be included in the amniotes or limnoscelids and should be considered a nomen dubium.

As in the other two diadectomorph families, virtually all of our understanding of the family Diadectidae is based on a single genus, the highly specialized, Permo–Pennsylvanian *Diadectes,* which is represented by large numbers of excellently preserved specimens (Olson, 1947, 1950; Berman et al., 1992). Only two other extremely rare, earlier occurring Late Pennsylvanian genera are known well enough to be included confidently in this family. One of these, *Diasparactus zenos,* is known by a nearly complete skeleton that includes a fragmentary skull and differs from *Diadectes* in only a few minor ways (Case and Williston, 1913). The other genus, *Desmatodon,* which is the subject of this report, is even more poorly known, containing two species that are represented by very fragmentary remains from only two (Case, 1908; Romer, 1952; Vaughn, 1969, 1972) or possibly three (Fracasso, 1980; Berman, 1993) North American localities.

The holotype of the type species of *Desmatodon, D. hollandi,* was originally described by Case (1908) on the basis of a fragment of left maxilla (CM 1938) containing four complete teeth and the root of a fifth, although several chevron bones were also referred to the species. These elements, as well as isolated bones of an eryopid amphibian, edaphosaurid early synapsid, and diadectid, were collected at Pitcairn, approximately 15 miles east of Pittsburgh, Pennsylvania, from the Upper Pennsylvanian Red Knob Formation (originally Pittsburgh Red Shale), about midlevel in the Conemaugh Group. The strong similarity of the teeth of the holotypic jaw to the unusual molariform cheek teeth of the Lower Permian *Diadectes* was noted by Case (1908), who considered those of *D. hollandi* as more primitive. Romer's (1952) redescription of the fragmentary left maxilla of *D. hollandi* also emphasized the similarity of its teeth to those of *Diadectes,* noting that the teeth of *Desmatodon* are more primitive in their lesser degree of molarization.

It was not until over a half century later that new material of the poorly known *Desmatodon* was reported. In 1969 and 1972 Vaughn described several isolated cranial and postcranial elements of a new species, *D. hesperis,* from a highly fossiliferous Late Pennsylvanian site that he discovered in the Sangre de Cristo Formation near the town of Howard in the Arkansas River Valley of Fremont County, central Colorado. In their review of late Paleozoic tetrapod faunas and localities, Milner and Panchen (1973) designated this new locality the "Badger Creek locality." The Badger Creek quarry has yielded an amazingly diverse fauna. In addition to the diadectomorph *Desmatodon hesperis,* Vaughn (1969, 1972) described a xenacanth shark and paleoniscoid fish, labyrinthodont amphibians, the aistopod amphibian *Coloraderpeton brilli* Vaughn (1969), the microsaur amphibian *Trihecaton howardinus* Vaughn (1972), and several early synapsids that include an ophiacodont, a sphenacodontid, *Edaphosaurus* aff. *E. raymondi,* and *Edaphosaurus* cf. *E. ecordi.* Berman and Sumida (1990) described a new species of diadectomorph limnoscelid, *Limnoscelis dynatis,* based on a nearly complete, disarticulated skeleton that was part of Vaughn's Badger Creek quarry collections. The Badger Creek quarry early synapsid remains, as well as new, unreported specimens, were restudied by Sumida and Berman (1993), who identified one member each of the families Ophiacodontidae, Sphenacodontidae, and Haptodontidae, and two members of the Edaphosauridae, one referable to *Ianthasaurus* (Reisz and Berman, 1986). Primarily on the basis of its vertebrate assemblage, but also utilizing geological work of Mallory (1958, 1960), Vaughn (1969, 1972) estimated the age of the Badger Creek quarry deposit as Late Pennsylvanian, most probably Missourian.

From the Badger Creek *Desmatodon* material, Vaughn (1969) selected a nearly entire left maxilla with a complete dentition as the holotype of *D. hesperis.* Although Vaughn pointed out that its maxillary dentition is essentially similar to that in *D. hollandi,* he recognized as the principal feature distinguishing the two species the tendency toward a more primitive, conical-shaped tooth structure in *D. hesperis.* Additional elements of *D. hesperis,* including a braincase with some attached dermal roofing bones and a maxilla, were recovered and described by Vaughn (1972) from the Badger Creek quarry. Subsequent to this description Vaughn recovered more material referable to *D. hesperis,* none of which has been described except for an isolated left atlantal neural arch (Sumida et al., 1992). Importantly, this material includes cranial elements of *Desmatodon* that not only provide a more complete knowledge of its morphology, but perhaps a better understanding of its phylogenetic relationships.

The *D. hesperis* material described here is part of much larger collections of vertebrates made by Peter P. Vaughn from the Permian and Pennsylvanian of southwestern United States and originally catalogued with the University of California, Los Angeles, vertebrate paleontology collections. In 1987, through the generosity of Peter P. Vaughn, these collections were permanently transferred to the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. The following abbreviations are used to refer to repositories of specimens: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts; UCLA VP, University of California, Los Angeles; UCMP, Museum of Paleontology, University of California, Berkeley; YPM, Yale Peabody Museum, New Haven, Connecticut.

DESCRIPTION

The undescribed cranial material of *Desmatodon hesperis* from the Badger Creek quarry includes: a left premaxilla (CM 47678); the approximate anterior

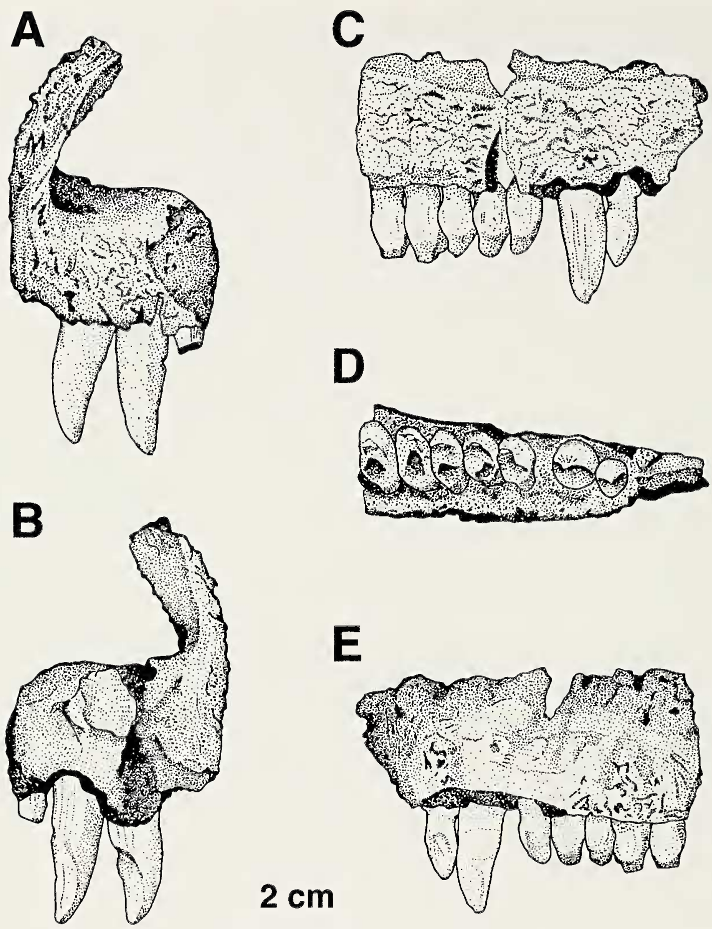

Fig. 1.—*Desmatodon hesperis.* A, B, lateral and medial views of left premaxilla CM 47678. C–E, lateral, dorsal, and medial views of anterior half of right maxilla CM 47677.

half of a right maxilla containing the first seven teeth (CM 47677); the greater portions of an articulated right pterygoid and quadrate and closely associated dorsal and caudal vertebra preserved in a single large block, a nearly entire lower right jaw with an almost complete dentition, and the posterior end of a left jaw that includes the glenoid region of the articular and portions of the surangular and prearticular surrounding the adductor fossa (CM 47670); a right palatine (CM 47674); a nearly entire left dentary with complete dentition (CM 47676); and a partial right pterygoid (CM 47673) questionably assigned to this species. With the exception of the maxilla and quadrate the cranial elements listed above are described here for the first time in *Desmatodon.*

The left premaxilla CM 47678 (Fig. 1) is nearly complete. The massive rostral body is subrectangular in lateral view and supports a long, narrow dorsal process that is missing perhaps only about 1 cm of its distal tip. There is only a slight narrowing of its distal half. The weak posterodorsal curvature of the dorsal process suggests a deep, bluntly rounded snout. The premaxilla holds four teeth: the first tooth, represented by an empty aveolus whose lingual wall is absent, was at least as large as the succeeding two teeth. The second and third teeth are complete and subequal in size, project vertically from the ventral margin of the premaxilla, and are distinctly incisiform. Their bases or proximal thirds are oval in horizontal section, with their long axes directed posteromedially, whereas the posterolingual surfaces of their distal portions are slightly and broadly concave, giving them a chisel-like appearance in lateral view. All that remains of the fourth tooth is its base, which is round in horizontal section with a diameter slightly greater than half that of the preceding two teeth. Surface sculpturing of the premaxilla consists of a rather coarse, granular texture with no definite pattern, becoming slightly more accentuated on the dorsal process, where there are minute, scattered, tubercular prominences. A step-like, semicircular depression on the lateral surface of the posterior margin of the rostral body of the premaxilla indicates the area overlapped by the premaxillary process of the maxilla.

The partial right maxilla CM 47677 (Fig. 1) consists of approximately the anterior half of the element and includes the anteriormost seven teeth, which are all well preserved. Anterior to the first tooth is a thin, anteriorly directed, flange-like extension of the lateral surface of the maxilla, the premaxillary process, that overlapped the lateral surface of the premaxilla. CM 47677 is slightly larger than the holotype CM 47654 (formerly UCLA VP 1706), a nearly entire maxilla containing a complete dentition of 12 teeth and believed to represent an adult (Vaughn, 1972). The adult condition of both maxillae is indicated by their overall dimensions and the sizes of their teeth. Using the transverse width of the seventh tooth as a means of comparison, that in the holotype is 7.8 mm, whereas that in CM 47677 is 9.3 mm. Vaughn (1972) also described a much smaller, nearly entire right maxilla (CM 47688; formerly UCLA VP 1748) with a complete dental series of eight teeth as belonging to a juvenile. Although the dentition of CM 47677 described here more closely matches that in the holotypic maxilla than that in the referred juvenile maxilla, it exhibits some similarities to both. The teeth in CM 47677 are slightly larger in width than those in the holotype, yet they are more closely packed with slightly shorter spaces between them. The first seven teeth in CM 47677 are contained in a length of 3.5 cm, compared to 4.2 cm in the holotypic maxilla. As Vaughn (1972) noted, although the dental row of eight teeth in the juvenile maxilla occupies a length only slightly less than that occupied by the first eight teeth in the holotype, the teeth in the juvenile specimen are all much shorter in anteroposterior length but are separated by much larger gaps. In all three specimens the first two teeth are alike in more closely approaching the incisiform structure of the premaxillary teeth than the molariform structure of the succeeding maxillary cheek teeth; they differ strongly, however, in their overall size and degree of incisiform development. The first two teeth in the holotype are much wider but only slightly longer than those of the rest of the series. In CM 47677 the first tooth is slightly longer but narrower and the second is markedly longer and wider than those of the rest of the series. This gives the second tooth the appearance of being caniniform in lateral view, yet most of its distal lingual surface is slightly and broadly excavated. In the juvenile maxilla the first two teeth are strongly incisiform, being moderately bowed lingually and narrower, but twice as long as those of the rest of the series (Vaughn, 1972). The posteriormost five cheek teeth of the partial maxilla CM 47677 exhibit a gradual increase in molarization posteriorly in the series. Anteriorly the crowns are like those described by Vaughn (1969, 1972) in the holotypic left maxilla CM 47654.

Table 1.—*Maximum crown measurements (in mm) and ratios of largest preserved, midseries maxillary cheek teeth in selected specimens of* Desmatodon *and* Diadectes. *Tooth positions or probable positions noted in parentheses.*

	Maximum transverse width	Maximum anteroposterior length	Maximum height	Length/width	Height/width
Desmatodon hesperis					
CM 47654 (holotype) (positions 7 and 8)	7.8	5.3	8.5	0.68	1.09
Desmatodon hesperis					
CM 47677 (seventh, posteriormost preserved tooth)	9.3	4.5	8.0	0.48	0.86
Desmatodon hollandi					
CM 1938 (holotype) (?eighth, posteriormost preserved tooth)	9.5	4.3	7.0	0.45	0.74
Desmatodon					
Aff. *D. hollandi* YPM 8639 (CM 38044) (positions 9 to 11)	9.5	4.3	7.0	0.45	0.74
Diadectes lentus					
FMNH UC 675 (positions 6 to 8)	13.6	5.3	5.5	0.39	0.40

At the posterior end of the series, however, the crowns exhibit a greater degree of molarization than those of the holotype in three important ways (Table 1): 1) the central cusp becomes far less prominent, whereas the lingual cusp becomes more strongly developed; 2) the height of the crown becomes reduced from greater to lesser than the transverse width of the crown; and 3) the ratio of the anteroposterior length to the transverse width of the crown is greatly reduced. As in the holotype, however, the cheek teeth of CM 47677 are positioned very close together.

The greater portions of a right pterygoid and quadrate CM 47670 (Fig. 2) are preserved and articulated, but their full exposure is precluded by the close association of a dorsal and a caudal vertebra. Exposed almost entirely in medial view, the palatal ramus has the appearance of a nearly vertical plate, as near its dorsal margin it curves abruptly laterally. Most of the preserved medial surface of the palatal ramus is smoothly finished. This portion of the ramus curves very slightly ventromedially to end in a broadly arching border that lies a short distance above the narrow, ventromedial, ridge-like edge of the ramus. Short longitudinal ridges and scattered pits below the smoothly finished area represent the region of contact of the ramus with its mate. The narrow, ventromedial ridge-like edge of the palatal ramus is coarsely sculptured and supports a row of 19 well-developed teeth, many of which are preserved as impressions. The anterior preserved tooth appears to be the first tooth of the series in that, as the palatal ramus continues anteriorly a short distance, its nearly intact ventral edge quickly retreats dorsally without any signs of additional teeth. In the articulated palate, therefore, the paired pterygoids supported a double row of teeth along the midline. The teeth of the palatal ramus are alike, consisting of a cylindrical base with minute longitudinal striations and a sharply pointed conical crown. The teeth are approximately 0.5 mm in height except for the last eight exhibiting a marked decrease in height to about 0.05 mm.

The transverse flange of the pterygoid consists basically of a narrow, subtriangular plate that projects well below the level of the ventral margins of the palatal

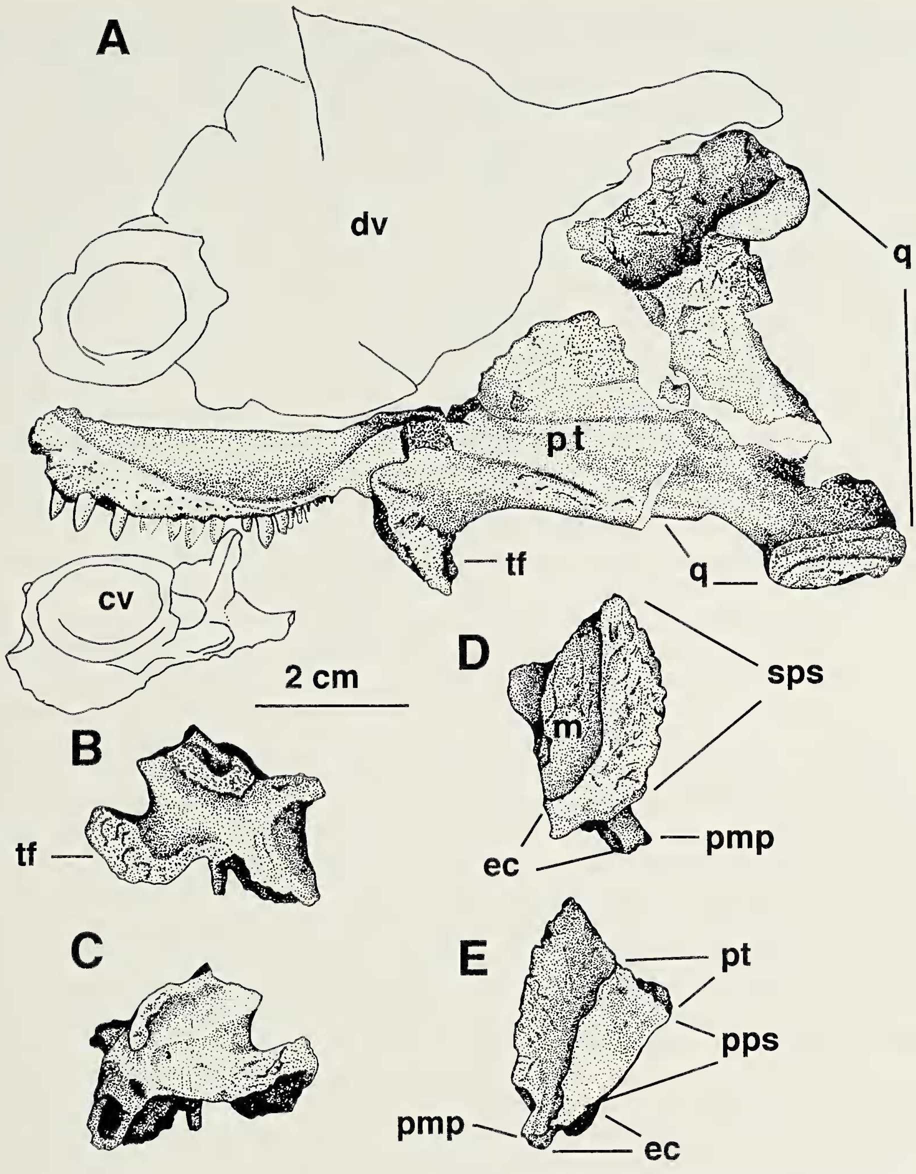

Fig. 2.—*Desmatodon hesperis.* A, medial view of articulated right pterygoid and quadrate with closely associated dorsal and caudal vertebrae CM 47670; B, C, ventral and dorsal views of partial right pterygoid CM 47673 missing palatal and quadrate rami (anterior toward top of page); D, E, ventral and dorsal views of right palatine CM 47674 (anterior toward top of page). Abbreviations: cv, caudal vertebra; dv, dorsal vertebra; ec, area of ectopterygoid contact; m, area of maxillary contact; pmp, posteromedial process; pps, primary palatal shelf; pt, pterygoid and area of pterygoid contact; q, quadrate; sps, secondary palatal shelf; tf, transverse flange.

and quadrate rami. The plane of its palatal or internal surface faces anteromedially and slightly ventrally. A well-developed, strongly rugose ridge, supporting a single row of ten small teeth with spaces for possibly two more, is aligned along the posteromedial edge of the palatal surface of the flange. The teeth are cylindrical with bluntly conical tips and increase in size, determined in part by impressions or the diameters of remaining bases, with increasingly more lateral position on the flange. The anteromedial corner of the flange is lost, but apparently would have been continuous with the laterally inflected lip of the dorsal border of the palatal ramus. Medial to the transverse flange the region of articulation with the braincase is also lost. The ventral margin of the vertical, wing-like quadrate ramus of the pterygoid is greatly thickened to form a smoothly rounded edge. Anteriorly the edge broadens and divides, with one branch extending slightly medially to the basicranial articulation region and the other extending laterally to nearly the toothed ridge of the transverse flange. There is no development of a medially projecting flange from the thickened ventral edge of the quadrate ramus, as seen in the diadectomorph *Limnoscelis* (Berman and Sumida, 1990). Above the thickened ventral edge the ramus becomes a thin sheet, the incomplete posterior margin of which was applied to the medial surface of the quadrate.

In his preliminary study notes, Vaughn identified a partial right pterygoid (CM 47673) (Fig. 2) as belonging to an adult of *Desmatodon hesperis* and consisting of only the region of the basipterygoid articulation. A noteworthy feature of this element is the absence of teeth on the transverse flange, which he believed might represent another dental difference between juvenile and adult specimens. Details of the morphology of this pterygoid, however, do not agree with the tooth-bearing pterygoid of *D. hesperis* (CM 47670) described above. Because an alternative identification cannot be offered, we have retained Vaughn's assignment of CM 47673 to *D. hesperis* as questionable.

The right quadrate articulated with the pterygoid (CM 47670) described above (Fig. 2) is badly fractured and incomplete, missing mainly the anterior third of the lateral facet of the ventral condyle and the posterior surface above the condyle that formed the anterior margin of the temporal or otic notch. It agrees in structure with the fragmentary remains of two right quadrates of *Desmatodon hesperis* (CM 47666 and 47667, formerly UCLA VP 1746 and 1747, respectively) described by Vaughn (1972) from the Badger Creek locality. The articular surface of the ventral condyle is divided into two subequal, anteroposteriorly elongated facets by a deep channel. The larger medial facet lies in direct line with the ventral edge of the quadrate ramus of the pterygoid. Above the ventral condyle the quadrate consists of a broad, subtriangular dorsal lamella, the posterior margin of which is poorly preserved. The posterior margin of the dorsal lamella is slightly concave in lateral view, but turns abruptly posteriorly just before reaching a dorsal condyle at its summit. The dorsal condyle has a medially facing facet that articulated with the prootic of the braincase (Watson, 1954).

The isolated palatine CM 47674 (Fig. 2) is so similar to that of *Diadectes* that there is no doubt as to its assignment to *Desmatodon*. An unusual feature of the palatine is the development of a pronounced, arcuate, secondary palatal shelf that extends medially from its contact with the inner margin of the maxillary alveolar shelf and ventral to the primary shelf of the palatine. A narrow, anteroposterior ridge distinctly marks the medial extent of the maxillary contact with the lateral portion of the ventral surface of the palatine. The exposed ventral surface of the secondary palatal shelf is distinctly sculptured by short, shallow, irregular channels and low ridges, and a few, scattered, minute tubercular prominences. The secondary palatal shelf of the palatine extends farther medially than the primary palatal shelf and a deep, medially opened channel is formed between them. The posterior end of the channel is nearly closed by a thick, ventrally rounded ridge that extends a short distance across the ventral surface of the primary shelf and then continues as a short posteromedial projection, referred to here as the posteromedial process; this process contacted the anterior margin of the transverse flange of the pterygoid. The ventral surface of the ridge on the primary palatal shelf, its posteromedial process, and the posterior third of the dorsal surface of the secondary palatal shelf are covered by a shagreen of denticles. The presence of minute denticles in this area of the palatine would seem to argue against the theory that the secondary palatal shelf represents a partially developed secondary palate (Olson, 1947).

If the relationships of the palatine to its neighboring elements is as in *Diadectes,* then the anterolateral margin of the primary palatal shelf contacted the pterygoid (Fig. 2). This area of the palate in *Diadectes* has not been fully described, even in the most recent descriptions (Olson, 1947), and if our interpretation is correct, it can be considered very likely that the pterygoid in *Desmatodon* not only prevented the palatine from contacting the vomer, but also formed a substantial portion of the posterior medial border of the internal naris. Furthermore, the pterygoid also contacted the entire medial margin of the primary palatal shelf. The ectopterygoid contact with the palatine was restricted to the area extending between the posterolateral end of the secondary palatal shelf and the lateral margin of the posteromedial process.

The lower jaw of *Desmatodon hesperis* is well represented in the undescribed material from the Badger Creek quarry. Particularly important is the nearly complete right lower jaw (CM 47670) which possesses an almost intact dentition (Fig. 3). Its most serious loss is the glenoid portion of the articular and most of the ventral lamina of the dentary on the lateral surface of the jaw. The jaw has suffered considerable mediolateral crushing. This has resulted in the thick alveolar shelf of the dentary protruding nearly a centimeter beyond the plane of the inner surface of the jaw and the dorsal margin of the lateral surface of the dentary protruding a half centimeter beyond the outer surface of the jaw. Sculpturing is confined to the lateral surface of the jaw and consists of an irregular pattern of fine grooves that grades into a coarser granular texture of very small, closely spaced, irregular protuberances.

The adductor fossa of CM 47670 is long and narrow, and opens mainly dorsally, as the medially bounding rim formed by the prearticular arches ventrally only slightly below the level of the lateral rim of the fossa. This condition, however, is contradicted by the posterior end of a left jaw CM 47670 (not illustrated), believed to belong to the same individual as the right jaw, because they were found closely associated and are of the appropriate size. In that jaw the medial rim of the fossa extends much farther below the level of the lateral rim. The large, anteroposteriorly elongate opening located about midlength along the medial surface of the right jaw CM 47670 is referred to here as the medial fenestra (Welles, 1941), although the alternative names of inframeckelian, Meckelian, and inframandibular fenestra or fossa have been used. Welles (1941) also identified in *Diadectes* a small anterior fenestra a short distance directly anterior to the medial fenestra that opens on the dentary–splenial suture, but noted its absence in a fragmentary jaw examined by him. He referred to this opening as the anterior

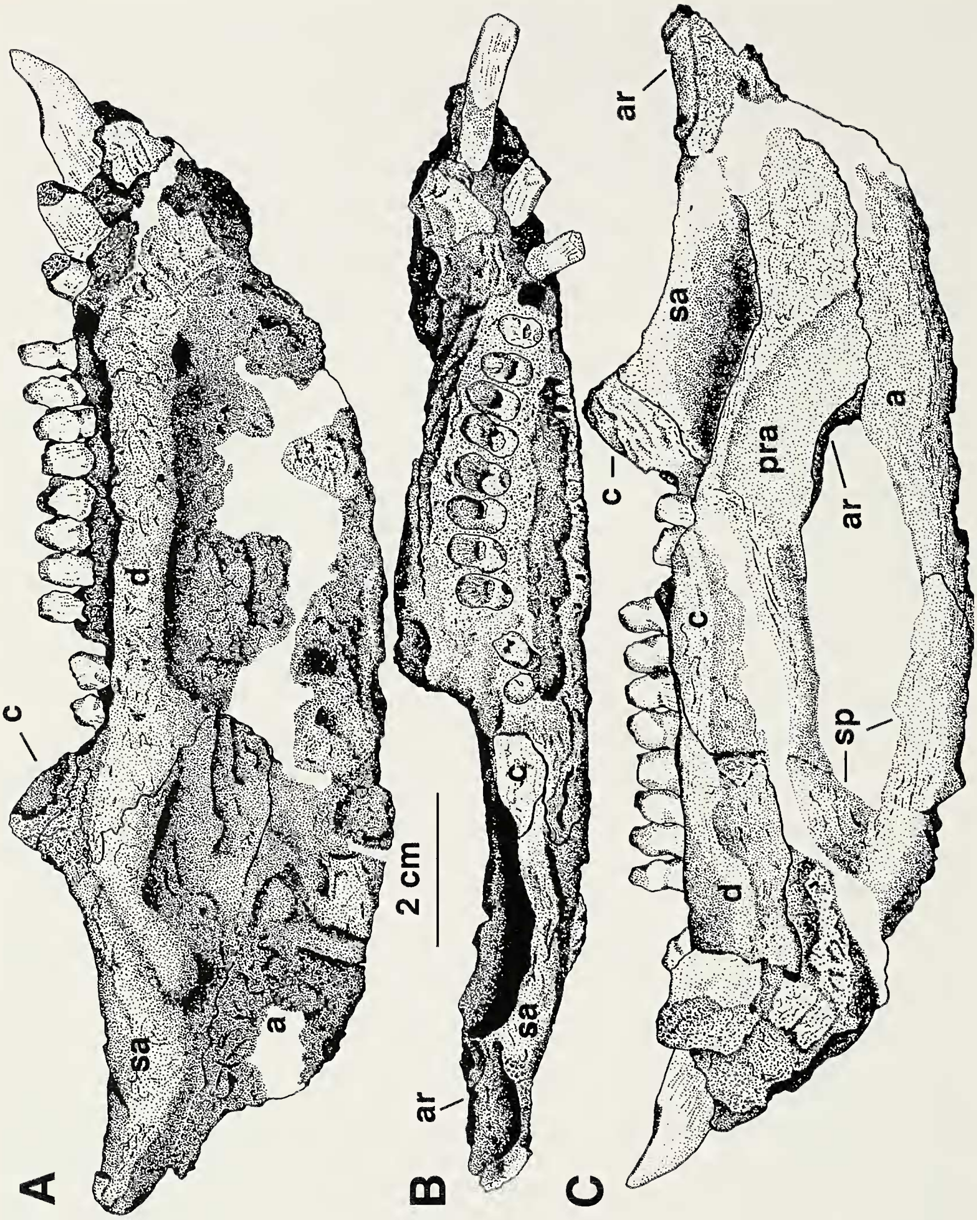

Fig. 3.—*Desmatodon hesperis* CM 47670. A–C, lateral, dorsal, and medial views of right lower jaw. Abbreviations: a, angular; ar, articular; c, coronoid; d, dentary; pra, prearticular; sa, surangular; sp, splenial.

fenestra and described it as communicating with the Meckelian canal or, as he preferred, the primordial canal. At the position of this fenestra in the *Desmatodon* right lower jaw CM 47670, the dentary and splenial are very narrowly separated, and the dentary margin has a smoothly rounded edge.

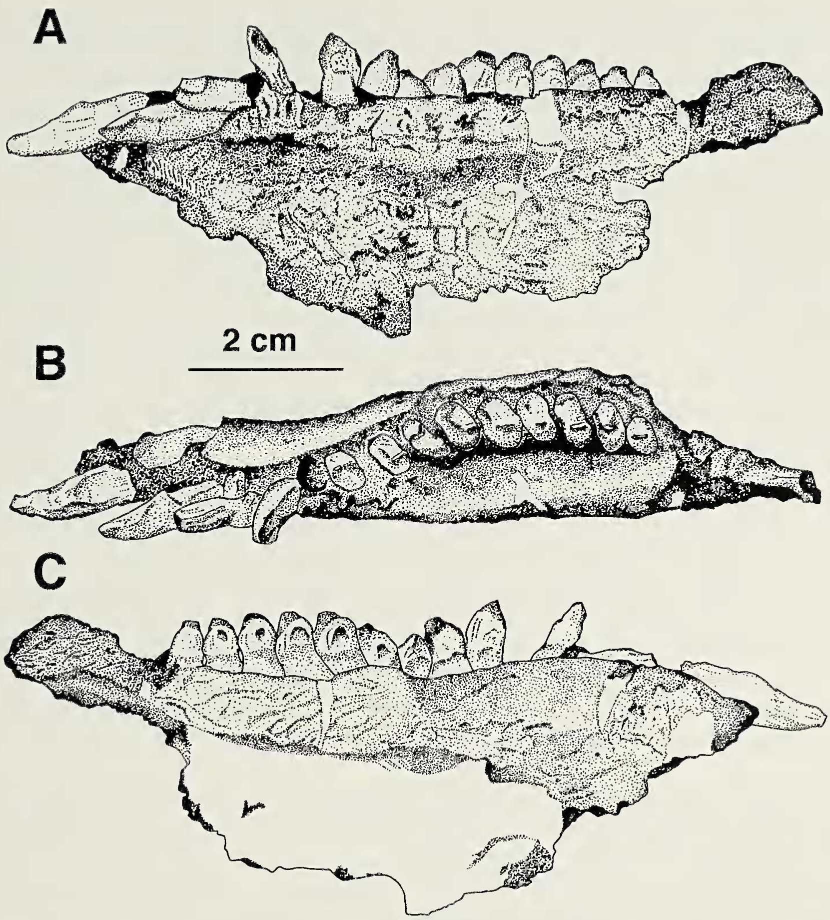

Fig. 4.—*Desmatodon hesperis* CM 47676. A–C, lateral, dorsal, and medial views of left dentary.

The dentary is represented by the complete right jaw CM 47670 and the nearly complete, isolated left dentary CM 47676 (Fig. 4). The two dentaries are seemingly the same length, 9.88 cm, but the teeth of the former are slightly larger, with the largest cheek teeth being about a millimeter greater in transverse width. Lateral to the bases of the cheek teeth is a shallow groove, the outer wall of which is formed by a vertical extension of the lateral surface of the dentary into a low, thin ridge or parapet. It is assumed that, as in *Diadectes,* the lateral surfaces of the parapet and lower jaw proper occupy the same plane. As already noted, however, the lateral surface below the parapet is depressed due to crushing in the right jaw CM 47670. The parapet is low, attaining a height throughout its length equal only to the level of the bases of the cheek teeth. In medial view the alveolar shelf, which in CM 47670 is covered posteriorly by the coronoid, exhibits a gradual, overall reduction in vertical depth of about 50% posteriorly. The dentary forms the greater part of the well-developed mandibular symphysis. Both dentaries possessed 14 teeth, with the fourth tooth in CM 47670 and the fifth tooth in CM 47676 represented by empty alveoli. The first three teeth are incisiform, and the fourth is intermediate in form between the anterior incisors and the posterior cheek teeth. The incisors decrease markedly in size posteriorly and are separated by wide spaces. The cheek teeth increase gradually in size posteriorly to about the eleventh tooth, then decrease markedly to the end of the series, and all are separated by very narrow spaces. The teeth have the same general morphology and wear patterns as those in *Diadectes* (Welles, 1941).

The coronoid is nearly complete in CM 47670, but has been broken into two pieces at the level of the posterior end of the maxilla by the mediolateral crushing of the jaw. An anterior, thin, flat, rectangular portion sheaths the posterior half of the medial surface of the alveolar shelf of the dentary, and in the absence of crushing would have contacted the prearticular along its ventral margin. The coronoid is incomplete anteriorly, reaching the level of the ninth tooth. Judging from a faint sutural scar on the alveolar shelf, however, it must have reached at least the level of the eighth tooth. A small, narrowly rectangular portion of the coronoid forms the coronoid eminence at the anterior end of the lateral margin of the adductor fossa, contacting the surangular on its posteroventral margin. Here the coronoid is visible in both lateral and medial views of the jaw and attains a dorsalmost level slightly above that of the cheek teeth. The remaining posterior portion of the lateral margin of the adductor fossa is formed by a smoothly rounded, thickened edge of the surangular that rises slightly anterodorsally in a broadly concave arc. Almost the entire margin of the surangular exposure is preserved on the lateral surface of the right jaw. Just below the coronoid the anterior margin of the surangular is deeply incised by the dentary, forming a strongly sigmoid suture between them. The surangular appears to have extended to the posterior limit of the jaw, obscuring the entire glenoid region of the articular from lateral view.

The splenial is exposed on both the lateral and medial surfaces of the jaw, as it forms the ventral keel of the anterior portion of the jaw. Poor preservation, however, prevents description of the narrow extent of the splenial along the ventral margin of the lateral surface of the jaw, where its dorsal margin contacts the dentary. On the medial surface of the jaw the splenial forms a small to moderate portion of the coarsely textured, thickened symphyseal surface. From here it continues posteriorly as a smoothly finished surface that divides after a short distance to enclose the anterior end of the medial fenestra. A narrow, dorsal band forms the anterior fourth of the dorsal border of the fenestra. The posterior margin of the band contacts the prearticular, but its dorsal margin has been displaced laterally by crushing from its contact with the anterior end of the ventral margin of the alveolar shelf of the dentary; it may have also had a very narrow contact with the anteroventral corner of the coronoid. The ventral, posterior extension of the splenial forms the anterior half of the ventral margin of the medial fenestra and ends in a contact with the angular.

The glenoid surface of the articular of the partial, posterior end of left jaw CM 47676 is nearly complete, consisting of a pair of laterally facing facets that are separated by a low keel. The complete lateral or dorsal facet is anteroposteriorly oval in outline, and, whereas much of the perimeter of the medial or ventral facet is incomplete, the two facets appear to have been comparable in size, outline, and orientation. A mediolaterally flattened, blade-like anterior process of the articular extends anteriorly from the anterolateral edge of the medial facet and is applied to the lateral surface of the prearticular. In medial view of the right jaw CM 47670 it is visible only as a very narrow band along the posterior end of the dorsal margin of the medial fenestra. In the posterior end of the left jaw CM 47676 (not illustrated) a proximal, disjunct portion of the anterior process of the articular is preserved. It extends between the adductor fossa and the medial fenestra and is almost entirely exposed in lateral view due to the incomplete preservation of the surangular. The partially preserved prearticular, however, covers all but a narrow, ventral portion of the medial surface of the process as in CM 47670. The absence of the surangular at this level indicates that the dorsal margin of the anterior process of the articular nearly reaches the adductor fossa.

Although the extent of the angular on the lateral surface of the right jaw CM 47670 is poorly preserved, it clearly occupied a large oblong area at the posteroventral corner of the jaw ventral to the surangular. A narrow portion of its posterior margin that laterally overlapped the articular is lost, whereas its poorly defined anterior margin apparently reached a level just beyond the surangular. In medial view the angular forms the posterior half of the ventral margin of the medial fenestra. From the extreme posterior corner of the fenestra to the incomplete posterior angle of the jaw it has a nearly horizontal, dorsal sutural margin that first broadly contacts the prearticular, then narrowly contacts the articular. The prearticular is exposed on the medial surface of the jaw as a smooth, flat, strap-like element; only its posterior contact with the articular is lost. It forms the entire ventromedial border of the adductor fossa. Anteriorly there is a marked reduction in its vertical width as it contacts the ventral margin of the coronoid (separated by the mediolateral crushing of the jaw CM 47670) and forms a large central portion of the dorsal margin of the medial fenestra.

Comparisons and Discussion

Desmatodon hesperis *and* D. hollandi.—The new material of *Desmatodon hesperis* described here provides a limited basis for reviewing the specific diagnosis given by Vaughn (1969) for this species, inasmuch as the holotype and only identified specimen of *D. hollandi* (CM 1938) consists of only a fragment of left maxilla with four teeth and the root of a fifth. As noted in the preceding description, the last four teeth in the anterior half of the right maxilla CM 47677 of *D. hesperis* (tooth positions three through seven) exhibit several gradual changes posteriorly in the series toward a greater degree of molarization. Most importantly, these changes more or less bridge the gap between the primitive state of molarization seen in the holotypic maxilla of *D. hesperis* and the more advanced state seen in the holotype of *D. hollandi*. Direct comparison between CM 47677 and the holotype of *D. hollandi* is facilitated by the fact that their dentitions include teeth from nearly the same region of the maxillary series. The four complete teeth of the holotype of *D. hollandi* are undoubtedly from near the anterior end of the maxillary series and likely include, as Vaughn (1969:17) determined, the fifth through eighth and the root of the ninth. In contrast to the holotypic maxilla of *D. hesperis,* the posteriormost preserved cheek tooth in the maxilla CM 47677 essentially matches those at the posterior end of the preserved series in the holotype of *D. hollandi*. This is a result of the following changes in the crown morphology of CM 47677 (Table 1): 1) reduction in height, not only absolutely, but also relative to the increased transverse width, resulting in a crown height-to-width ratio of 0.86 for the seventh tooth compared to 0.74 for the probable eighth tooth in the holotype of *D. hollandi*; 2) reduction in anteroposterior length, not only absolutely, but also relative to the increased transverse width, resulting in a crown length-to-width ratio of 0.48 for the seventh tooth compared to 0.45 for the probable eighth tooth in the holotype of *D. hollandi*; and 3) concomitant with the two preceding changes is a reduction in the prominence of the central cusp and an increased development of the lingual cusp. The degree of molarization of the midseries cheek teeth in the lower jaw CM 47670 and the isolated dentary CM 47676 of *D. hesperis* is also comparable to that in the holotypic maxilla of *D. hollandi.*

Greater maturity undoubtedly accounts for the greater degree of molarization of the cheek teeth in the *D. hesperis* maxilla CM 47677 compared to those in the holotypic maxilla CM 47654. The maxilla CM 47677 is larger than that of the holotype of *D. hesperis* and closer in overall size to the still larger holotypic maxilla of *D. hollandi.* It should also be recalled from the preceding description that with increasing size of the maxillae of *D. hesperis* are pronounced changes in the dentition other than degree of molarization. Still, it is unknown whether an individual of *D. hesperis* attaining the same size as the holotype of *D. hollandi* would possess cheek teeth of equivalent molarization.

Two other characters used by Vaughn (1969:13) to distinguish the two species of *Desmatodon* remain unchallenged by the new material of *D. hesperis*: 1) in *D. hesperis* the lingual wall of the maxilla does not extend as far ventrally as the labial wall, permitting a greater exposure of the tooth bases on the lingual side, whereas in *D. hollandi* the lingual and labial walls extend to about the same level; and 2) in *D. hesperis* the cheek teeth are set very close together, whereas in *D. hollandi* the spacing between a pair of teeth is equal to almost half of the anteroposterior length of the tooth bordering the space anteriorly. The validity of the latter comparison applies only to maxillae in adult specimens of comparable size, because, as described above, the spacing of the cheek teeth in the much smaller juvenile maxilla of *D. hesperis* CM 47677 is very large and probably relatively greater than that in *D. hollandi.*

Juveniles of Desmatodon *and* Diadectes.—As our understanding of the cranial morphology of *Desmatodon* grows, it becomes increasingly evident that the features which distingush it from the very closely related *Diadectes* are in the dentition. In this paper, but more so in that by Vaughn (1972), it has been pointed out that there are several dramatic changes in the maxillary dentition of *D. hesperis* in the transition from juvenile to adult. Vaughn (1972) also noticed that some of these developmental changes are not known to occur in *Diadectes* specimens of any growth stage. The availability of some extremely small, juvenile specimens of *Diadectes,* as well as adult specimens comparable in size to those of *D. hesperis,* allows the recognition of possibly two classes of differences between the maxillary and dentary dentitions of *Desmatodon* and *Diadectes*: 1) *Desmatodon* exhibits juvenile stages of dental development that are not present in juvenile specimens of *Diadectes,* and 2) *Desmatodon* and *Diadectes* exhibit dental differences as adults. In the following comparison of the dentitions of *Desmatodon* and *Diadectes* two important assumptions are made. Firstly, it is assumed that, despite the limited number of known *Desmatodon* specimens, the considerably larger, overall sizes commonly attained by *Diadectes* specimens compared to those of *Desmatodon* reflect an actual difference in the maximums of their size ranges. If this assumption is accepted, then it is reasonable to conclude also that when comparing similarly sized specimens of both genera, those of *Diadectes* may represent relatively less mature individuals. Secondly, it is nec-

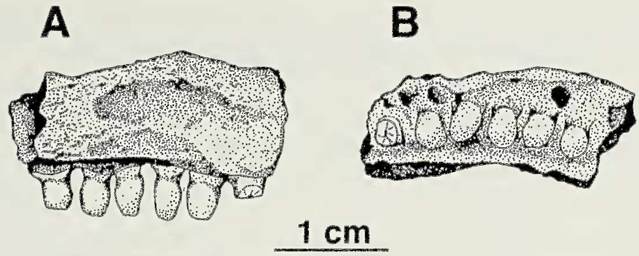

Fig. 5.—*Diadectes* sp. MZC 2780. A, B, lateral and dorsal views of partial, right juvenile maxilla.

essary to assume that the largest *Desmatodon* specimens represent nearly or fully adult individuals.

The juvenile *Desmatodon hesperis* maxilla CM 47668 exhibits at least four dental features which are absent or greatly reduced in mature specimens of this genus and apparently not present in specimens of *Diadectes* species of any age; these were discussed by Vaughn (1972) and are more fully documented here: 1) fewer number of teeth, 2) greater relative spacing of teeth, 3) first two maxillary teeth relatively longer and more incisiform, and 4) absence of wear facets. The juvenile maxilla CM 47668 of *D. hesperis* possesses only eight teeth, which are separated by very wide gaps, in a length of 42 mm. By way of contrast with *Diadectes,* Vaughn (1972) noted that in the skull of the immature specimen *Diadectes sanmiguelensis* MCZ 2989, from the Lower Permian Cutler Formation of Colorado (Lewis and Vaughn, 1965), the maxilla possesses a total of 11 teeth and empty alveoli in the much shorter span of about 36 mm. The spaces between the teeth are also relatively much shorter, usually about one half or less, than those in the juvenile *Desmatodon* CM 47668. Apparently, a larger number of maxillary teeth set more closely together appears much earlier in juvenile specimens of *Diadectes.* This is dramatically illustrated in a large collection of undescribed, isolated maxillae and dentaries and mainly disarticulated postcranial elements of several extremely small individuals of *Diadectes* from the Early Permian of Texas that are collectively catalogued as MCZ 2780 without specific assignment. Included in the collection is a pair of very small maxillae, measuring 45 and 48 mm in preserved length, that consist almost entirely of the alveolar shelf and the bases of the teeth. Each possesses 12 very closely spaced teeth in a length of only 39 mm, which is within the 11 to 13 range found in adults specimens of *Diadectes.* It was emphasized by Vaughn (1972) that the first two teeth in the juvenile maxilla of *D. hesperis* (CM 47668) differ from those in the adult holotype (CM 47654) in being relatively much longer and more incisiform in structure; thus, they more closely resemble the incisors of the premaxilla than the succeeding maxillary cheek teeth. Although the partial maxilla of *D. hesperis* CM 47677 is slightly larger than the holotype, its second tooth is considerably longer, giving it a strongly caniniform appearance. The first two maxillary teeth are poorly preserved in almost all of the juvenile specimens of *Diadectes* at hand. However, the first two teeth of the maxillae in the immature specimen of *D. sanmiguelensis* (MCZ 2989) are complete enough to state, as Vaughn (1972) had, that they are more like the cheek teeth of the maxilla in their length and crown structure than the incisors of the premaxilla. This is even truer in mature specimens of *Diadectes.* Lastly, Vaughn (1972) noted the remarkable absence of wear facets on any of the teeth in the juvenile *D. hesperis* maxilla CM 47668, whereas distinct facets are found on most of the teeth of the adult maxillae of this species. Vaughn (1972) speculated that these changes in the maxillary dentition in the transition from juvenile to adult specimens of *D. hesperis* reflect a shift in dietary habits.

It is important to point out here that the maxillary and dentary cheek teeth in the very immature specimens of *Diadectes* MCZ 2780 and *D. sanmiguelensis* MCZ 2989 exhibit a strikingly lesser degree of molarization than that seen in mature specimens of the genus. In general, the cheek teeth in these juvenile specimens (Fig. 5) show little or no transverse widening, but rather are bulbous, with a weakly developed central cusp and essentially no lingual or labial cusps. In these features the maxillary cheek teeth in extremely small or very immature specimens of *Diadectes* differ from those in the somewhat larger and presumably more mature juvenile specimen of *Desmatodon hesperis* CM 47688. The lack of specimens of appropriate sizes, however, makes it impossible to determine whether this initial stage in the development of the cheek teeth in *Diadectes* also occurs in *Desmatodon.* The incisiform teeth of the premaxilla and the dentary in *D. hesperis* and *Diadectes* do not exhibit any noticeable changes in their morphology in the transition from juvenile to adult and appear to be similar in the two genera.

Adults of Desmatodon *and* Diadectes.—If the *Desmatodon hesperis* maxillae CM 47654 and 47677 and the nearly complete lower jaw CM 47670 are considered to belong to adult or nearly adult specimens, then it can be stated that their cheek teeth do not exhibit the same advanced degree of molarization as that seen in adult specimens of *Diadectes.* This is especially evident when the dentitions in the above *D. hesperis* specimens are compared with those in comparably sized specimens of *Diadectes.* Among the specimens at hand, the nearly complete skull and left lower jaw of *Diadectes lentus* FMNH UC 675 from the Permo–Pennsylvanian of New Mexico best exemplify the greater molarization of the cheek teeth in this genus compared to that in comparably sized specimens of *D. hesperis.* The *Diadectes* skull FMNH UC 675 is 17 cm or sightly greater in overall length and is clearly that of an adult; its maxillae have an estimated length of about 70 mm and possess 11 teeth and empty alveoli each. Although the 77 mm-long holotypic maxilla of *D. hesperis,* possessing 12 teeth, suggests a greater overall skull size than that of FMNH UC 675, its cheek teeth exhibit a far lesser degree of molarization (Table 1). In FMNH UC 675 the crowns of the largest preserved, midseries maxillary cheek teeth (positions 6 to 8) have the following maximum measurements: transverse width 13.6 mm, anteroposterior length 5.3 mm, and height 5.5 mm. The corresponding maximum measurements for the largest cheek teeth (positions 7 and 8) in the holotypic maxilla of *D. hesperis* are 7.8, 5.3, and 8.5 mm, respectively. Direct comparisons of these measurements clearly indicate a much more molariform structure of the cheek teeth in FMNH UC 675 than in CM 47654, as the crowns of the former are over 70% wider and shorter, and nearly 50% lower. The greater molarization of the crowns in FMNH UC 675 can also be expressed in terms of their considerably smaller length-to-width and height-to-width ratios of 0.39 and 0.40 compared to those of 0.68 and 1.09, respectively, calculated for the holotypic maxilla of *D. hesperis.* As already noted, the partial *D. hesperis* maxilla CM 47677 is slightly larger than the holotypic maxilla in overall size, and the crown of its largest and posteriormost preserved tooth, the seventh, exhibits an even greater degree of molarization than the cheek teeth in the holotype. In addition to the crown of the seventh tooth in CM 47677 having a greater transverse width of 9.3 mm, its anteroposterior length of 4.5 mm

Table 2.—*Maximum crown measurements (in mm) and ratios of largest preserved, midseries dentary cheek teeth in selected specimens of* Desmatodon *and* Diadectes. *Tooth positions or probable positions noted in parentheses.*

	Maximum transverse width	Maximum anteroposterior length	Maximum height	Length/width	Height/width
Desmatodon hesperis	8.8	4.7	7.0	0.53	0.80
Desmatodon hesperis					
CM 47661 (isolated crown)	10.5	5.7	6.8	0.54	0.65
Diadectes lentus					
FMNH UC 675 (probable positions 8 to 10)	11.6	4.7	5.5	0.41	0.47

and height of 8.0 mm are less than the maximums for these measurements in the holotypic maxilla; conversion of these measurements to the length-to-width and height-to-width ratios of 0.48 and 0.86, respectively, also indicates a relatively shorter and lower crown (Table 1). Concomitant with the increased width and the decreased height of the crowns of the cheek teeth in FMNH UC 675 is an increased development of the lingual cusp and a reduced prominence of the central cusp.

As in the comparisons made with the maxillae above, although the right lower jaw of *Desmatodon hesperis* CM 47670 is slightly larger than that in *Diadectes* FMNH UC 675—their lengths being 14.94 and 13.32 cm, respectively—similar contrasting measurements of the cheek teeth demonstrate a greater degree of molarization in the latter (Table 2). Maximums for the transverse width, anteroposterior length, and height of the crowns of the largest cheek teeth (positions 9 to 11) in CM 47670 are 8.8, 4.7, and 7.0 mm, respectively, whereas the corresponding measurements for the largest cheek teeth (probably positions 8 to 10) in FMNH UC 675 are 11.6, 4.7, and 5.5 mm. Not only are the transverse widths of the crowns greater in FMNH UC 675, but also shorter and lower relative to the width, with length-to-width and height-to-width ratios of 0.41 and 0.47, respectively, compared to 0.53 and 0.80 for the same ratios in CM 47670. In addition, accompanying the increased width and the decreased height of the crowns in FMNH UC 675 are a pronounced increase in the development of the labial cusp and a reduction in the prominence of the central cusp.

Approximately 18 isolated teeth of *Desmatodon hesperis* have been collected from the Badger Creek quarry, indicating the probable presence of several individuals other than those represented by the described maxillae and dentaries. Yet, only one of the teeth, a cheek tooth (CM 47661; formerly UCLA VP 1713), is noticeably larger than those of the preserved dentitions. It was described by Vaughn (1969) as probably belonging to a dentary. The crown measures 10.5, 5.7, and 6.8 mm in transverse width, anteroposterior length, and height, respectively, giving it a more molariform structure than the cheek teeth in the *D. hesperis* lower jaw CM 47670 (Table 2). Not only is the absolute width of the isolated crown CM 47661 greater, but its height-to-width ratio of 0.65 is smaller; on the other hand, length-to-width ratios for the two specimens are essentially equal. Yet, the degree of molarization of the crown CM 47661 still does not approach that demonstrated by the cheek teeth in the *Diadectes* dentary FMNH UC 675, as determined by the same criteria used above.

Two other important dental characters further distinguish *Desmatodon hesperis* and *Diadectes.* Most importantly, the transverse flange of the pterygoid in *D. hesperis* CM 47670 possesses a single row of small teeth supported by a well-developed, rugose ridge, whereas in *Diadectes* the transverse flange is smoothly finished and lacks teeth of any size. The pterygoid CM 47670 is at least as large as that in the adult *Diadectes* skull FMNH UC 675, which lacks teeth on the transverse flange. This would seem to eliminate the possibility that the presence of teeth on the transverse flange of the pterygoid in *D. hesperis* is a juvenile feature. In addition, the medial margin of the ventral surface of the palatal ramus of the pterygoid CM 47670 supports a row of 19 well-developed teeth that vary considerably in size. On the other hand, this tooth row in *Diadectes* FMNH UC 675 includes only half as many teeth that vary little in size and are relatively larger.

If the lower jaws of *Desmatodon hesperis* CM 47670 and *Diadectes* FMNH UC 675 belong to adults of comparable sizes, then two striking, nondental differences can be used to distinguish them. Most notably, the jaw of CM 47670 is much shallower, as are its medial fenestra and adductor fossa. By way of comparison, the right lower jaw of CM 47670 has a height (5.00 cm, measured at the highest level of the coronoid)-to-length (14.94 cm) ratio of nearly 1:3, whereas in *Diadectes* FMNH UC 675 the same measurements of its higher (6.67 cm) but slightly shorter (length 13.32 cm) right jaw yield a ratio of nearly 1:2. Essentially the same 1:2 ratio was calculated for the larger lower jaws of *Diadectes* specimens UCMP 33903 and 59023 (from the Lower Permian of New Mexico and Texas, respectively), having lengths of 16.3 and 25.5 cm, respectively. The second feature of the lower jaw distinguishing *Desmatodon* and *Diadectes* is the development of the labial parapet lateral to the bases of the cheek teeth. In CM 47670 the labial parapet is much lower and is the same height throughout its length. As a result, all of the cheek teeth are visible in lateral view, whereas in the lower jaw of *Diadectes* FMNH UC 675 there is decreasing visibility of the crowns from full exposure anteriorly to complete concealment at about midlength in the series and farther posteriorly. The preceding features of the lower jaw of *Diadectes* FMNH UC 675 become more pronounced in larger specimens of the genus, whereas the contrasting features in *D. hesperis* CM 47670 are seen in *Diadectes* only in the very small lower jaw (length 8.8 cm) of the juvenile specimen *D. sanmiguelensis* MCZ 2989.

New Synapomorphy of Desmatodon *and* Diadectes.—The articulars of the lower jaws of *Desmatodon hesperis* CM 47676 and 47670 were described as possessing a very unusual anterior process extending from the anterolateral edge of the medial facet. The mediolaterally flattened, blade-like process contacts the lateral surface of the prearticular, so that in the nearly complete right lower jaw CM 47670 its exposure is limited to a very narrow strip along the the posterodorsal border of the medial fenestra. Welles (1941) described the identical structure of the articular in *Diadectes* as nearly reaching the posterior end of the alveolar shelf of the dentary. In the very large left lower jaw (length 25.5 cm) of *Diadectes* UCMP 59023 from the Lower Permian of Texas the anterior process of the prearticular extends to the level of the anterior end of the dorsal border of the medial fenestra. It would appear that the structure of the articulars in *Diadectes* and *Desmatodon* are not only identical, but unique among all Paleozoic tetrapods in their possession of this long anterior process.

Basicranial Articulation in Desmatodon *and* Diadectes.—In Vaughn's (1972:

22–23) description of the braincase of the immature specimen of *Desmatodon hesperis* (CM 47665; formerly UCLA VP 1746) he notes that the basipterygoid process has smooth anterodorsal and anteroventral articular surfaces that are directed anteriorly and laterally and that the joint between the braincase and palate was obviously mobile. He contrasted this with the firmly joined condition in *Diadectes,* citing the description by Olson (1947). The possession of a mobile basicranial joint was interpreted by Vaughn (1972) as a possible primitive feature of *D. hesperis,* noting, however, that it might also represent another sign of immaturity of the specimen. His latter suspicion appears to be the correct interpretation, inasmuch as this feature can also be demonstrated in a partial, disarticulated skull of a juvenile specimen of *Diadectes* (CM 38047) from the Permo–Pennsylvanian of New Mexico (Berman et al., 1992). The basipterygoid articular surfaces of its disarticulated basiparasphenoid are quite distinct, joining at a right-angle margin of the process so as to be divided into nearly equal anteriorly and laterally facing facets. This approximates the condition in *D. hesperis* CM 47665. In mature specimens of *Diadectes* at hand the basicranial joint appears to be firmly fused.

Status of Desmatodon *aff.* D. hollandi *from New Mexico.*—Fracasso (1980) reported what he believed to be the first record of *Desmatodon* aff. *D. hollandi* from the Late Pennsylvanian Cutler Formation of El Cobre Canyon, north-central New Mexico. This was based on a tooth-bearing right premaxilla and maxilla and some badly crushed skull fragments YPM 8639. A silastic rubber cast of this specimen (CM 38044) indicates a size appropriate for comparison (Table 1) of its maxillary dentition with those in *Desmatodon hesperis* (CM 47654 and 47677), the holotype of *D. hollandi* (CM 1938), and the *Diadectes lentus* skull FMNH UC 675. Maximum measurements for the transverse width, anteroposterior length, and height of the crowns of the largest cheek teeth (positions 9 to 11) of the New Mexico specimen of *Desmatodon* YPM 8639 are 9.5, 4.3, and 7.0 mm, respectively, and convert to length-to-width and height-to-width ratios of 0.45 and 0.74, respectively. These figures compare closely with those for the partial maxilla of *D. hesperis* CM 47677 and in particular the holotypic maxilla of *D. hollandi.* In addition, the cheek teeth in YPM 8639 also more closely duplicate those in the above specimens of *D. hesperis* and *D. hollandi* in the lesser development of the lingual cusp and the greater prominence of the central cusp. The anterior two maxillary teeth of YPM 8639, however, more closely match those in *D. lentus* FMNH UC 675 and this genus in general by their greatly reduced height and a morphology more like that of the succeeding cheek teeth than the incisiform teeth of the premaxilla. YPM 8639 is not preserved well enough, however, to determine whether the ventral extent of the lingual wall of the maxilla, as utilized by Vaughn (1972), is more like that of *D. hesperis* or *D. hollandi.* The spacing between the cheek teeth in YPM 8639, however, is closer to that in *D. hollandi* than that in *D. hesperis.* If YPM 8639 does pertain to *Desmatodon,* then it should probably be referred to *D. hollandi,* as Fracasso (1980) argued.

CONCLUSIONS

1. Differences in the degree of molarization of the maxillary cheek teeth previously used to distinguish *Desmatodon hesperis* and *D. hollandi* may reflect differences in maturity and, therefore, cannot be considered a reliable taxonomic character; however, the greater ventral extent of the lingual wall of the maxilla

and the greater spacing between maxillary cheek teeth still appear to be valid criteria for distinguishing *D. hollandi* from *D. hesperis.*

2. The cranial morphologies of *Desmatodon* and *Diadectes* are essentially alike except for their dentitions and perhaps a few proportional differences in the lower jaws of adult specimens.

3. The juvenile maxillary dentition of *Desmatodon hesperis* differs from that of *Diadectes* at any growth stage by the following characters (Vaughn, 1972): 1) fewer teeth, 2) greater spacing of teeth, 3) first two teeth relatively longer and more incisiform, and 4) absence of wear facets.

4. The maxillary and dentary dentitions of comparably sized, adult specimens of *Desmatodon hesperis* and *Diadectes* can be distinguished by the greater degree of molarization of the cheek teeth in the latter, as expressed in the following features: 1) the crowns are transversely wider, and their anteroposterior length-to-width and height-to-width ratios are smaller; 2) the lingual cusps of the maxillary and the labial cusps of the dentary cheek teeth are more strongly developed; and 3) the prominence of the central cusps is reduced. Further, in contrast to the condition in *D. hesperis* the first two maxillary teeth in *Diadectes* are greatly reduced in height and are more like the succeeding cheek teeth than the incisiform teeth of the premaxilla.

5. The presence of teeth on the transverse flange and twice as many teeth of smaller and variable sizes forming the single medial row on the palatal ramus of the pterygoid also distinguishes *Desmatodon hesperis* from *Diadectes.*

6. The adult lower jaw of *Desmatodon hesperis* differs from that of comparably sized *Diadectes* specimens in being much shallower, as are its adductor fossa and medial fenestra, and in having a much lower labial parapet.

7. The long, mediolaterally flattened, blade-like anterior process of the articular that is applied to the lateral surface of the prearticular and is almost completely hidden from medial view by that bone is a feature unique to *Diadectes* and *Desmatodon,* and possibly all diadectids, among late Paleozoic tetrapods.

8. Fracasso's (1980) report of *Desmatodon* aff. *D. hollandi* from the Late Pennsylvanian Cutler Formation of El Cobre Canyon, New Mexico, may represent only the second occurrence for the species and the third for the genus.

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LITERATURE CITED

BAIRD, D., AND R. L. CARROLL. 1967. *Romeriscus,* the oldest known reptile. Science, 157:56–59.

BERMAN, D. S. 1993. Lower Permian vertebrate localities of New Mexico and their assemblages. Pp. 11–21, *in* Vertebrate Paleontology of New Mexico (S. G. Lucas and J. Zidek, eds.), New Mexico Museum of Natural History and Science, Bulletin 2, 338 pp.

BERMAN, D. S, AND S. S. SUMIDA. 1990. A new species of *Limnoscelis* (Amphibia, Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo Formation of central Colorado. Annals of Carnegie Museum, 59:303–341.

BERMAN, D. S, S. S. SUMIDA, AND R. E. LOMBARD. 1992. Reinterpretation of the temporal and occipital regions in *Diadectes* and the relationships of diadectomorphs. Journal of Paleontology, 66:481–499.

CARROLL, R. L. 1967. A limnoscelid reptile from the Middle Pennsylvanian. Journal of Paleontology, 41:1256–1261.

CASE, E. C. 1908. Description of vertebrate fossils from the vicinity of Pittsburgh, Pennsylvania. Annals of Carnegie Museum, 4:234–241.

CASE, E. C., AND S. W. WILLISTON. 1913. Description of a nearly complete skeleton of *Diasparactus zenos* Case. Carnegie Institution of Washington, Publication 181, 81 pp.

FRACASSO, M. A. 1980. Age of the Permo–Carboniferous Cutler Formation vertebrate fauna from El Cobre Canyon, New Mexico. Journal of Paleontology, 41:1256–1261.

———. 1987. Braincase of *Limnoscelis paludis* Williston. Postilla, 201:1–22.

GAUTHIER, J. A., A. G. KLUGE, AND T. ROWE. 1988. The early evolution of the Amniota. Pp. 103–155, *in* The Phylogeny and Classification of the Tetrapods, Volume 1, Amphibians, Reptiles and Birds (M. J. Benton, ed.), Systematics Association, Special Volume 35A, Clarendon Press, Oxford, 377 pp.

LANGSTON, W., JR. 1966. *Limnosceloides brachycoles* (Reptilia: Captorhinomorpha), a new species from the Lower Permian of New Mexico. Journal of Paleontology, 40:690–695.

LAURIN, M., AND R. R. REISZ. 1992. A reassessment of the Pennsylvanian tetrapod *Romeriscus*. Journal of Vertebrate Paleontology, 12:524–527.

———. 1995. A reevaluation of early amniote phylogeny. Zoological Journal of the Linnean Society, 113:165–223.

LEWIS, G. E., AND P. P. VAUGHN. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville area, Colorado. Contributions to Paleontology, Geological Survey Professional Paper, 503-C:1–46.

MALLORY, W. W. 1958. Pennsylvanian coarse arkosic redbeds and associated mountains in Colorado. Pp. 17–20, *in* Rocky Mountain Association of Geologists, Symposium on Pennsylvanian Rocks of Colorado and Adjacent Areas.

———. 1960. Outline of Pennsylvanian stratigraphy of Colorado. Pp. 23–33, *in* Guide to the Geology of Colorado, Geological Society of America and Rocky Mountain Association of Geologists.

MILNER, A. R., AND A. L. PANCHEN. 1973. Geographical variation in the tetrapod faunas of the Upper Carboniferous and Lower Permian. Pp. 353–368, *in* Implications of Continental Drift to the Earth Sciences, Volume 1 (D. H. Tarling and S. K. Runcorn, eds.), Academic Press, London.

MOSS, J. L. 1972. The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseajaia campi* Vaughn (Amphibia: Seymouriamorpha). University of California, Publications in Geological Sciences, 98:1–72.

OLSON, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana, Geology, 7:2–53.

———. 1950. Relationships of *Diadectes*. Fieldiana, Geology, 14:199–227.

PANCHEN, A. L., AND T. R. SMITHSON. 1988. The relationships of the earliest tetrapods. Pp. 1–32, *in* The Phylogeny and Classification of the Tetrapods, Volume 1, Amphibians, Reptiles and Birds, (M. J. Benton, ed.), Systematics Association, Special Volume 35A, Clarendon Press, Oxford, 377 pp.

REISZ, R. R., AND D. S BERMAN. 1986. *Ianthasaurus hardestii* n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas. Canadian Journal of Earth Sciences, 23:77–91.

ROMER, A. S. 1946. The primitive reptile *Limnoscelis* restudied. American Journal of Science, 244: 149–188.

———. 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh–West Virginia region. Annals of Carnegie Museum, 33:47–110.

———. 1964. *Diadectes* an amphibian? Copeia, 4:718–719.

SUMIDA, S. S., AND D. S BERMAN. 1993. The pelycosaurian (Amniota, Synapsida) assemblage from the Late Pennsylvanian Sangre de Cristo Formation of central Colorado. Annals of Carnegie Museum, 62:293–310.

SUMIDA, S. S., R. E. LOMBARD, AND D. S BERMAN. 1992. Morphology of the atlas–axis complex of the late Paleozoic tetrapod suborders Diadectomorpha and Seymouriamorpha. Philosophical Transactions of the Royal Society of London, Series B, 336:259–273.

VAUGHN, P. P. 1964. Vertebrates from the Organ Rock Shale of the Cutler Group, Permian of Monument Valley and vicinity, Utah and Arizona. Journal of Paleontology, 38:567–583.

———. 1969. Upper Pennsylvanian vertebrates from the Sangre de Cristo Formation of central Colorado. Contributions in Science, Los Angeles County Museum of Natural History, 164:1–28.

———. 1972. More vertebrates, including a new microsaur, from the Upper Pennsylvanian of central Colorado. Contributions in Science, Los Angeles County Museum of Natural History, 223:1–30.

WATSON, D. M. S. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bulletin of the Museum of Comparative Zoology, 111:297–449.

WELLES, S. P. 1941. The mandible of a diadectid cotylosaur. University of California Publications in Geological Sciences, 25:423–432.

WILLISTON, S. W. 1911*a*. A new family of reptiles from the Permian of New Mexico. American Journal of Science, 31:378–398.

———. 1911*b*. American Permian Vertebrates. University of Chicago Press, Chicago, Illinois, 145 pp.